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SEPARATION AND REDESCRIPTION OF *HORMAPHIS HAMAMELIDIS* (FITCH 1851) AND *HORMAPHIS CORNU* (SHIMER 1867) (HOMOPTERA: APHIDIDAE) ON WITCH-HAZEL IN THE EASTERN UNITED STATES

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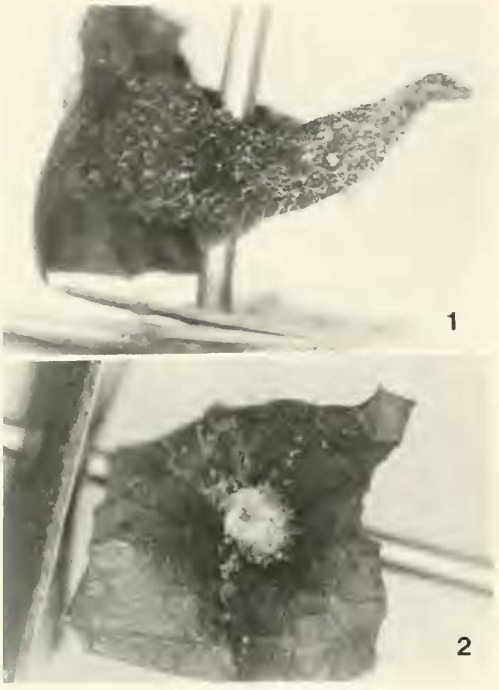
Abstract.—The taxonomic history of the genus *Hormaphis* and its nominate species, *H. hamamelidis* is reviewed. Two distinct species of aphids, previously grouped under the name *Hormaphis hamamelidis* (Fitch), are now recognized and redescribed. While both species form conical galls on the leaves of witch-hazel, each has a different life cycle and geographic distribution. *Hormaphis hamamelidis* (Fitch) is found in northern and high elevation regions of eastern United States and has an autoecious, 3-generation life cycle. The first complete description of all developmental stages is provided. *Hormaphis cornu* (Shimer) is confined to low elevations in the mid-Atlantic and southern regions of the United States, and its 7-generation life cycle includes host-alternation between witch-hazel and river birch. Six distinct forms of *Hormaphis cornu* are redescribed. In addition, it is established that all other known species currently placed in the tribe Hormaphidini belong to the genus *Hamamelistes.*

Key Words: taxonomic history, conical galls, hosts

The taxonomy of North American Hormaphidini has been confused at both the generic and specific levels. The first species described in this tribe was an aphid inhabiting cone-shaped galls (Figs. 1, 2) on the upper surface of witch-hazel (*Hamamelis virginiana* L.) leaves in New York State. Fitch (1851) gave it the name *Brysocrypta hamamelidis.* Few morphological characters were provided, the alates mistakenly were described as males, and both the generic name and that of its author, Haliday, were misspelled. Furthermore, it is unclear why the aphid was placed in this genus, because the diagnostic characters of *Byrsocrypta* Haliday include attributes such as 3 simple discoidals on the forewing, 2 simple discoidals on the hindwing, and 6-jointed antennae—none of which represent the aphid in question.

Except for the 1851 paper by Fitch, the taxonomy of North American Hormaphidini has comprised only two genera, *Hormaphis* Osten-Sacken (1861) and *Hamamelistes* Shimer (1867). At present, the genera are separated by two characters: (1) the number of antennal segments in alates (*Hormaphis* with 3 and *Hamamelistes* with 5) and (2) the presence or absence of a cubitus vein in the hindwing (*Hormaphis* with cubitus vein absent and *Hamamelistes* with cubitus vein present).

The genus *Hormaphis* was first proposed by Osten-Sacken in 1861 for his new species, *Hormaphis hamamelidis,* an aphid collected from conical galls on witch-hazel near



Figs. 1, 2. *Hormaphis hamamelidis* type 871, follicle. 1, Cone-shaped gall. 2, Tufted opening at bottom of gall.

Washington, D.C. Osten-Sacken noted only that the antennae had ring-like sensoria and indistinguishable joints in the last segment, and that the cubitus veins in the forewing were joined in a fork. Walsh (1867) speculated that Osten-Sacken was unaware of Fitch's 1851 publication and the use of the specific epitaph *hamamelidis,* and that Osten-Sacken's use of the identical specific name was coincidental.

Working with Illinois populations, Shimer (1867) described two new species of aphids on witch-hazel in his new genus, *Hamamelistes.* He named the aphid from conical or horn-like leaf galls *Hamamelistes cornu,* and described the alates as having 3-jointed antennae with approximately 36 sensoria on the third antennal segment; the conical galls were ½ to ⅞ inches in height and sometimes constricted at the base. The aphid from spiny flower galls he named *Hamamelistes spinosus,* and described the alates as having 5-jointed antennae. While his paper was in press, Shimer saw Fitch's 1851 publication but dismissed any connection between the aphids because of the generic characteristics of *Byrsocrypta.*

Oestland's (1887) treatment of *Hormaphis* Osten-Sacken stated that the antennae were 5-jointed and the hindwing had a cubitus vein; he included also a description of his new species *H. papyraceae.* In fact, the genus Oestlund described is *Hamamelistes* Shimer (1867) and his new species *H. papyraceae* is the birch form of the host-alternating *Hamamelistes spinosus* Shimer (1867).

Hormaphis was mentioned several other times in the early literature in keys or brief descriptive notes, in which it seemed to encompass either both genera, or to describe the current concept of *Hamamelistes*: e.g. antennae 3- to 5-jointed (Thomas 1877) or hindwing with 1 cubitus vein and antennae 5-jointed (Sanborn 1904, Jackson 1907). Thomas (1877) catalogued the aphid from conical galls twice: (1) as *Pemphigus hamamelidis* Fitch with a copy of Fitch's original sparse description, claiming that it appeared to be closely related to *Pemphigus,* but noting that the aphid might prove identical to *Hormaphis hamamelidis* Osten-Sacken, and (2) as *Hormaphis hamamelidis* Osten-Sacken, listing a few characters of the gall alate such as hindwing with one discoidal vein and (inexplicably) 3- to 5-jointed antennae.

In his extensive work on both *Hormaphis* and *Hamamelistes,* Pergande (1901) settled the confusion over distinction of the two genera by reporting that the developmental forms of every generation of *Hormaphis* had only 3 antennal segments and that alates had only a medius vein in their hindwings (see Pergande 1901, fig. 5). The alates of *Hamamelistes,* on the other hand, had 5 antennal segments and hindwings with both medius and cubitus veins (see Pergande 1901, fig. 16).

Tullgren (1909) concurred with Pergande's (1901) work on the generic diag-

nosis based on antennal segmentation. Mordvilko (1909) also separated the genera with this character, and most later keys (Börner 1930, Palmer 1952) distinguish *Hormaphis* and *Hamamelistes* by the number of antennal segments as well as hindwing venation.

While previous authors had examined only gall inhabitants, Pergande (1901) described the complete life cycles of both the cone-gall and spiny-gall aphids near Washington, D.C. He discovered both species were host-alternating between witch-hazel and river birch (*Betula nigra* L.), and completed seven and six clonal generations, respectively. From uncleared material, Pergande described all developmental forms of the aphids, calling the cone-gall aphid *Hormaphis hamamelidis* (Fitch), and the spiny flower-bud gall aphid *Hamamelistes spinosus* Shimer.

After studying populations of the cone-gall aphid in New York state, Morgan and Shull (1910) questioned whether the heteroecious cycle as described by Pergande (1901) applied to aphid populations in their region. In Cold Spring Harbor, alates emerging from galls contained sexual embryos and did not migrate; thus Morgan and Shull (1910) surmised that birch apparently was not an obligate secondary host. Based on Morgan and Shull's (1910) publication only and without further descriptive information, Börner (1952) gave the autoecious aphid the new name, *Hormaphis shulliana.*

To answer questions raised by Morgan and Shull (1910) about the life cycle of the cone-gall aphid, von Dohlen and Gill (1989) conducted a comparative study of *Hormaphis* aphids in Virginia and other parts of the eastern U.S. They found that populations at low elevations in low latitudes (south of approximately 36°N) followed the 7-generation, host-alternating life cycle that Pergande (1901) had described, but that populations at high elevations and northern latitudes had the much reduced autoecious cycle of only the fundatrix, alate sexuparae, and sexuales, noted by Morgan and Shull (1910). Autoecious and heteroecious aphids were found together only at one site in Maryland, 50 km northwest of Washington, D.C. In further work, it was established that both host-alternating and autoecious populations retained their respective life cycles when transplanted to the opposite environment (von Dohlen and Gill, in prep.). Ovip-

Figs. 3, 4. *Hormaphis hamamelidis* fundatrix. 3, 1st instar. 4, Adult.

arae and males from the different populations interbred readily (von Dohlen and Gill 1989), but no viable offspring resulted from hybrid matings (von Dohlen and Gill, in prep.).

The evidence above on geographic distributions of autoecious and host-alternating aphids and genetic stability of life cycles, coupled with the morphological differences described here, indicate that aphids with the different life cycles are indeed separate species.

In this paper we describe all developmental stages (fundatrix, sexupara, and sexuales) of the newly recognized and never adequately described autoecious species, whose proper name is *Hormaphis hamamelidis* (Fitch) (see below). Because the most complete description of the host-alternating species, whose correct name is *Hormaphis cornu* (Shimer) (see below), was from uncleared specimens (Pergande 1901), we redescribe this species for better comparison to *H. hamamelidis*.

Materials and Methods

Hormaphis aphids on witch-hazel and river birch were studied in the eastern United States from 1986–1989. *Hormaphis hamamelidis* was collected in Virginia from two highland sites, both at 1000 m elevation: the George Washington National Forest (Rockingham County) and the Shenandoah National Park, Central Section (Rappahannock County). *Hormaphis cornu* was collected at lowland sites in the Dranesville District Park, Dranesville, Virginia, close to Pergande's original study site, and at the U.S. National Arboretum in Washington, D.C.

Populations were sampled two to four times per month throughout the growing season (April to October at the highland sites and March to November at the lowland sites). Specimens were cleared in KOH and mounted in balsam or were mounted live in Hoyer's mounting medium.

Measurements of 28–30 individuals per morph were made with a ZIDAS (Zeiss Interactive Digital Analysis System) and a compound microscope.

Hormaphis Osten-Sacken, 1861

Hormaphis hamamelidis Osten-Sacken, 1861 = *Hormaphis cornu* (Shimer, 1867).
Hormaphidula Börner, 1952, type species *Hormaphis betulae* (Mordvilko, 1901) = *Cerataphis betulae* Mordvilko, 1901.

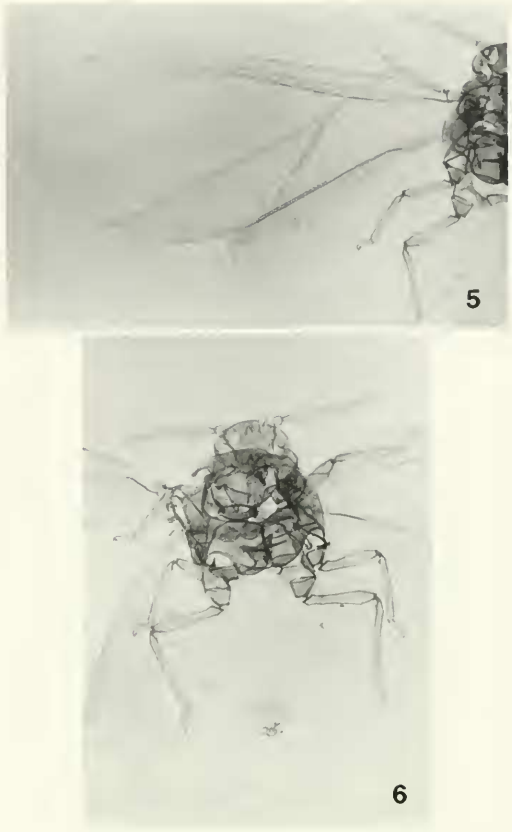
The genus *Hormaphis* Osten-Sacken is characterized by having in all developmental forms 3-segmented antennae and no cornicles, and in alates only a medius vein in the hindwing.

Hormaphis hamamelidis (Fitch 1851)

Brysocrypta hamamelidis Fitch, 1851.
Hormaphis hamamelidis (Fitch): Morgan & Shull, 1910.
Hormaphis shulliana Börner, 1952.
Hormaphis hamamelidis (Fitch): von Dohlen and Gill (1989) [in part].

Description: **Fundatrix** (Figs. 3, 4): First instar (Fig. 3). Body length 0.35–0.38 mm, width 0.19–0.21 mm. Dorsal wax pores large, in medial and marginal rows. On abdomen, dorsomedial wax pores usually limited to 1 pair each on segments 3 and 4 and to a single pore each on segments 6 and 7. Adult (Fig. 4). Color in life dark purple-brown, broadly oval. Eye a triommatidion. Apterous, body length 0.9–1.3 mm, width 0.7–0.9 mm. Dorsal cephalic setae length 0.9–1.4 × middle width antennal segment III (antIII). Two pairs of thoracic spiracles; 2–3 pairs abdominal spiracles. Two pairs wax glands on dorsum, one each between 1st and 2nd, 2nd and 3rd coxae. Cornicles absent. Antenna 3-segmented; segments I and II about equal in length and each with 2 setae, segment III 0.12–0.18 mm long and 2.0–3.2 × length hind tarsal segment II (tIIh) with 3 short thumb-like projections ventrally near apex and 4 short thick apical setae which are 0.4–0.7 × middle width antIII. Rostrum (segments II–V), length 0.8–

1.2 × length antIII, reaching almost to 2nd coxa, rostral segment II with 6 setae, III with 4 setae; apical rostral segment (ars) width: length 0.6–0.9 and 0.9–1.3 × length cauda, bearing 8 setae; longest seta 0.3–0.5 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.15–0.22 mm long with 6 setae in a circle around the apex and 3–5 additional along its length; longest tibial seta 0.8–1.3 × middle width tibia. Hindleg femur length 0.9–1.1 × length tibia with 2 short setae on the anterior margin, 2 thick, blunt and 2 longer setae on apical margin and 1–4 additional setae. Hindleg tarsal segment II 0.04–0.07 mm long and 0.26–0.35 × length tibia, with (all legs) 2 pair short setae and apically 2 long thick capitate setae (length 0.53–0.94 × length tIIh) and 2 thinner shorter tapered setae. Length femur foreleg 0.78–0.93 × femur hindleg, setae as in hindleg, tibia foreleg 0.65–0.80 × tibia hindleg, setae as in hindleg except only 1–2 in addition to 6 apical. Length femur midleg 0.81–0.94 × hindleg femur, setae as in hindleg except only 1–2 additional, length tibia 0.70–0.80 × hindleg tibia, setae as in foreleg. Tarsal segment I (tI) setal pattern 2:2:2, longest seta tI hindleg 0.3–0.7 × length ventral margin tIh. Genital plate with 8–20 setae, longest seta 0.7–1.3 × longest caudal seta. Anal plate bilobed with 6 (rarely 5) setae each lobe, longest seta 0.7–1.3 × longest caudal seta. Cauda rounded, 2.0–3.2 × broad as long with 4–8 (usually 6) setae, longest seta 0.6–0.9 × length cauda.



Figs. 5, 6. *Hormaphis hamamelidis* sexupara. 5, Wing venation. 6, Whole body.

Sexupara (Figs. 5, 6, 24): Color in life: Thorax dark purplish brown to black; wings opaque, veins gray-brown. Eye, compound. Alate, body (Fig. 6) length 1.1–1.7 mm. Dorsal cephalic setae 5–14, longest 0.52–1.35 × constricted basal width antIII. Ventral cephalic setae 6–11. Two paris of thoracic spiracles; 4 pairs of spiracles on abdominal segments 3–6. Cornicles absent. Forewing (Fig. 5) 1.5–2.0 mm long, medius unbranched, width cu-1a 0.8–1.4 × width medius, width cu-1b 0.8–1.8 × medius. Hindwing (Fig. 5) 0.9–1.4 mm long with medius only, hooklets 2–3. Antenna 3-segmented; length segment I 0.8–1.3 × segment II and each with 2 setae, segment III 0.25–0.43 mm long and 3.5–5.6 × length tIIh and bearing 19–27 annular secondary sensoria (Fig. 24), 2 short sensory pegs ventrally near apex, and 4 short thick apical setae, longest 0.9–1.7 × constricted basal width antIII. Rostrum (segments II–V), length 0.35–0.53 × length antIII, reaching between 1st and 2nd coxae, setae as in fundatrix; ars width : length 0.6–1.3 and length 1.0–1.8 × length cauda, longest seta 0.2–0.6 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.29–0.36 in length with 6 setae in a circle around the apex and 10–30 additional along entire length; longest tibial seta 0.57–0.97 × middle width

tibia. Hindleg femur length 0.73–0.90 × length tibia, with 2 short setae on anterior margin, 2 thick, blunt and 2 longer tapered setae on apical margin, and 1–11 additional setae. Hindleg tarsal segment II 0.065–0.088 mm long and 0.20–0.28 × length hindleg tibia, with (all legs) 2 pair short setae and apically 2 long thick capitate setae (length 0.47–0.70 × length tIIh) and 2 thinner, slightly shorter capitate setae. Length femur foreleg 0.75–1.11 × femur hindleg, setae as in hindleg except 1–14 in addition to the 6 invariant; tibia foreleg 0.70–0.95 × tibia hindleg, setae as in hindleg except 9–28 in addition to 6 apical. Length femur midleg 0.73–0.99 × hindleg femur, setae as in hindleg except 8–13 in addition to 6 invariant; length tibia midleg 0.70–1.0 × hindleg tibia, setae as in hindleg except 12–26 in addition to 6 apical. Tarsal segment I setal pattern 3:3:2, longest seta tI hindleg 1.1–1.9 × length ventral margin tI. Genital plate with 17–35 setae; 6–16 secondary and 11–19 marginal setae (no obvious primary setae), longest seta 0.6–1.1 × longest caudal seta. Anal plate bilobed with 7–9 setae right lobe, 7–9 left, longest seta 0.8–1.3 × longest caudal seta. Cauda knobbed, 1.0–1.6 × broad as long with 8–10 setae, longest seta 0.7–1.2 × length cauda.

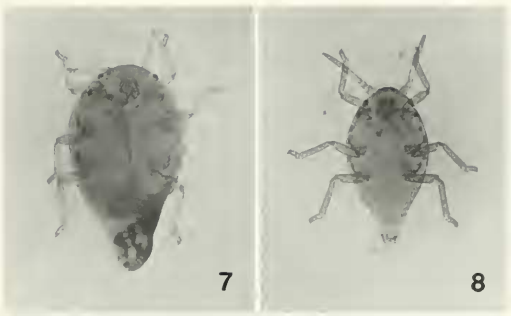
Ovipara (Figs. 7, 28): Color in life: Juvenile covered with fuzzy grayish wax secretions; adult shiny, purplish black. Apterous, body pyriform (Fig. 7), convex dorsally and flat ventrally, no tubercles or waxy secretions, highly sclerotized. Eye a triommatidion. Body length 0.66–0.83 mm, width 0.36–0.49 mm. Dorsal cephalic setae length 0.7–1.5 × middle width antIII. Dorsal setae thick, slightly capitate, ventral tapered. Two pairs of thoracic spiracles; 2–3 pairs abdominal spiracles. Two pairs wax glands, between 1st and 2nd, 2nd and 3rd coxae. Cornicles absent. Antenna 3-segmented; segments I and II about equal in length and each with 2 setae, segment III 0.13–0.20 mm long and 2.4–3.3 × length tIIh, with 2–3 short thumb-like projections ventrally near apex and 4 short thick projections on apex with length 0.50–0.82 × middle width antIII. Rostrum length 0.62–0.97 × length antIII, reaching almost to 2nd coxa, setae as in fundatrix; ars width : length 0.6–1.2, and 0.8–1.3 × length cauda, longest seta 0.2–0.7 × width ars. Coxae all legs with 6 setae. Tibia of hindleg 0.15–0.20 mm long with 7–19 pseudosensoria along entire length (Fig. 28); setae as in fundatrix except 2–8 in addition to apical 6, longest tibial seta 0.7–1.2 × middle width tibia. Hindleg femur length 0.77–0.94 × length tibia, setae as in fundatrix except 0–3 in addition to the 6 invariant. Hindleg tarsal segment II 0.046–0.065 mm long and 0.26–0.35 × length tibia, with (all legs) 2 pair short setae and apically 1 pair long thick capitate setae (length 0.57–0.79 × length tIIh) and 1 pair thinner, slightly shorter capitate setae. Length femur foreleg 0.83–0.99 × femur hindleg, setae as in hindleg; length tibia foreleg 0.74–0.88 × tibia hindleg, setae as in hindleg except 1–6 in addition to 6 apical. Length femur midleg 0.88–1.0 × hindleg femur, setae as in hindleg except 0–4 additional; length tibia midleg 0.78–0.88 × hindleg tibia, setae as in hindleg except 2–6 additional. Tarsal segment I setal pattern 3:3:2, longest seta tIh 1.3–2.6 × length ventral margin tIh. Genital plate with 13–23 setae, longest seta 0.6–1.7 × longest caudal seta. Anal plate bilobed with 8 (rarely 9) setae each lobe, longest seta 0.9–1.4 × longest caudal seta. Cauda knobbed, 1.0–1.5 × broad as long with 10 (rarely 12) setae, 2 longer than others, longest seta 0.7–1.3 × length cauda.

Male (Figs. 8, 26): Color in life: Juvenile and adult as in ovipara. Apterous, body dorsoventrally flattened (Fig. 8), elongated pyriform in shape, no tubercles or waxy secretions, highly sclerotized. Body length 0.45–0.60 mm, width 0.24–0.32 mm. Eye a triommatidion. Dorsal cephalic setae length 0.6–1.3 × middle width antIII. Setae shape as in ovipara. Two pairs wax glands as in ovipara, 1–2 pairs spiracles. Cornicles absent. Antenna 3-segmented; segments I and

II about equal in length and each with 2 setae, segment III (Fig. 26) 0.15–0.21 mm long and 3.3–4.7 × length tIIh, with 11–22 short sensory pegs ventrally along distal ~⅞ and 4 short thick projections on apex, length 0.41–0.71 × middle width antIII. Rostrum length 0.51–0.79 × length antIII, reaching between 2nd and 3rd coxae, setae as in fundatrix; ars width : length 0.7–1.2 and 1.0–1.8 × length cauda, longest seta 0.25–0.64 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.14–0.18 mm long, setae as in fundatrix except 3–6 in addition to apical 6, longest tibial seta 0.7–1.6 × middle width tibia. Hindleg femur length 0.80–0.94 × length tibia, setae as in fundatrix except 0–4 in addition to 6 invariant. Hindleg tarsal segment II 0.020–0.054 mm long and 0.24–0.36 × length tibia with setae as in ovipara; length thick capitate setae 0.61–0.90 × length tIIh. Length femur foreleg 0.83–1.0 × femur hindleg, setae as in hindleg except 0–2 in addition to 6 invariant; length tibia foreleg 0.75–0.91 × tibia hindleg, setae as in hindleg except 1–2 in addition to 6 apical. Length femur midleg 0.86–1.0 × hindleg femur, setae as in hindleg except only 0–1 additional; length tibia midleg 0.76–1.0 × hindleg tibia, setae as in foreleg. Tarsal segment I setal pattern 3:3:2, longest seta tIh 1.5–2.6 × length ventral margin tIh. Anal plate bilobed with 6 (rarely 8) setae each lobe, longest seta 0.5–1.2 × longest caudal seta. Cauda knobbed, 1.0–1.7 × broad as long with 6–10 setae, longest seta 0.7–1.2 × length cauda.

Overwintering egg: Pale orange yellow when first laid, then darkening to shiny black, 0.40 by 0.20 mm.

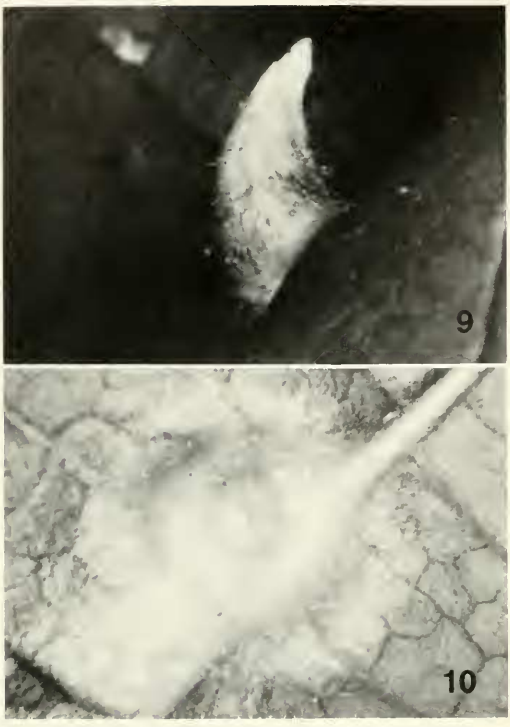
Gall: Conical with slight or no basal constriction, tip often bent to one side, protruding from upper leaf surface and usually on a major vein; length from tip to base on leaf underside 6.3–11.8 mm (mean = 8.1) and maximum width 3.1–5.5 mm (mean = 4.4). Base of gall on leaf undersurface circular and somewhat swollen beyond leaf surface, the circular opening at first obstructed by plant hairs, later forming a small exit hole. Color pale green, turning yellow.



Figs. 7, 8. *Hormaphis hamamelidis* sexuales. 7, Ovipara with eggs visible inside abdomen. 8, Male.

Biology: The host is *Hamamelis virginiana* L., witch-hazel, on which conical leaf galls can be found from May through September. Eggs hatch in mid-April, and first-instar fundatrices crawl to leaf buds. At bud break (early May) first-instar fundatrices start feeding on emerging leaves and galls begin to form. By mid-June fundatrices are mature, and they reproduce sexuparous nymphs through September. Alate sexuparae leave galls from late July to September and produce nymphs of sexuales directly onto the undersides of witch-hazel leaves. From early August until late September, oviparae and males are found on undersides of witch-hazel leaves where they mature (by late August) and mate. Each ovipara lays several eggs in bark crevices on the host plant, usually on older stems with more bark texture but occasionally at the base of leaf buds. Overwintering eggs are found on witch-hazel from September to April. See von Dohlen and Gill (1989) for additional information.

Types: Cotypes cited in Fitch 1851 and obtained from the New York State Museum, Albany: No. 869, male (actually a winged sexupara, and all that remains of the pointed specimen is the thorax with fragments of two wings and four legs); 870, larva (all that remains of the pointed specimen is an indistinguishable body); and No. 871



Figs. 9, 10. *Hormaphis hamamelidis* gall. 9, Cone-shaped gall. 10, Tufted opening at bottom of gall.

(Figs. 1, 2), follicle (the dried gall is in fairly good condition and measures 5.75 mm long and 2.5 mm wide with the tip bent to one side).

Material examined: Material collected on witch-hazel, George Washington National Forest (GWF), Rockingham County, VA, C. D. von Dohlen: fundatrices, 6 on 14 VI 1985, 23 on 14 VII 1987; sexuparae, 16 on 3 VIII 1985, 3 on 17 VII 1986, 22 on 9 VIII 1987; males, 8 on 15 IX 1986, 12 on 25 IX 1986; oviparae, 5 on 2 IX 1985, 35 on 25 IX 1986, 31 on 29 VIII 1988. Additional material collected on witch-hazel, Shenandoah National Park, Rappahannock County, VA, C. D. von Dohlen: fundatrix, 1 on 14 VI 1985; males, 6 on 12 IX 1986, 2 on 14 IX 1986.

Distinguishing characteristics: **Life cycle:** *Hormaphis hamamelidis* fundatrices mature in mid-June and persist until late September, and sexuparae leave galls from late July to late August, whereas *H. cornu* fundatrices mature in early May and live until mid-June, and their summer migrants depart galls in late May to mid-June. Sexuparae of *H. cornu* do not return to witch-hazel until mid September to late October. *Hormaphis hamamelidis* adult sexuales are found on witch-hazel leaves from late August to late September, while *H. cornu* sexuales are found from late September to late October. *Hormaphis hamamelidis* galls are generally smaller than those of *H. cornu* (height = 6.3–11.8 mm vs. 8.2–16.6 mm, respectively) and have little or no basal constriction; *H. cornu* galls are often constricted at the base. **Morphology:** *Hormaphis hamamelidis* fundatrices are smaller than *H. cornu* (0.9–1.3 mm vs. 1.32–1.98 mm) and more elongate rather than globular in shape. On the abdomen of the first instars of *H. hamamelidis* fundatrices, the dorsomedial wax pores usually are limited to 1 pair each on segments 3 and 4 and to a single pore each on segments 6 and 7, while the first instars of *H. cornu* fundatrices usually have 2 pairs each on segments 3 and 4 and 1 pair each on segments 6 and 7. *Hormaphis hamamelidis* sexuparae are distinguished from *H. cornu* alate viviparous females by wing length (1.5–2.0 mm and 1.9–2.2 mm, respectively), tibia length (0.29–0.36 mm vs. 0.35–0.44 mm, respectively). *Hormaphis cornu* sexuparae are more similar in size to *H. hamamelidis* sexuparae (though slightly smaller) and have similar numbers of secondary sensoria, but they have fewer setae on the genital plate (4–8 secondary and 4–13 marginal vs. 6–16 and 11–19 on *H. hamamelidis*), fewer setae on the foreleg tibia (8–18 vs. 15–34), middle leg femur (7–15 vs. 14–19) and tibia (9–20 vs. 18–32). *Hormaphis hamamelidis* oviparae are smaller than those of *H. cornu* (0.66–0.83 mm vs. 0.86–1.15 mm), antennal segment III is shorter (0.13–0.20 mm vs. 0.18–0.29 mm) and they have fewer sense plaques on the hindleg tibia (7–19 vs. 13–31). *Hormaphis*

hamamelidis males are also smaller (0.45–0.60 mm vs. 0.56–0.74 mm) with shorter hindleg tibia (0.14–0.18 mm vs. 0.18–0.21 mm).

Hormaphis cornu (Shimer, 1867)

Hamamelistes cornu Shimer, 1867.
Hormaphis hamamelidis Osten-Sacken, 1861 [secondary homonym of *Hamamelidis* Fitch 1851].
Hormaphis hamamelidis (Fitch): Walsh, 1867; Pergande, 1901; von Dohlen and Gill, 1989 [misidentifications].
Hormaphis hamamelidis Osten-Sacken: Thomas, 1877 [misidentification].
Pemphigus hamamelidis (Fitch): Thomas, 1877 [misidentification].

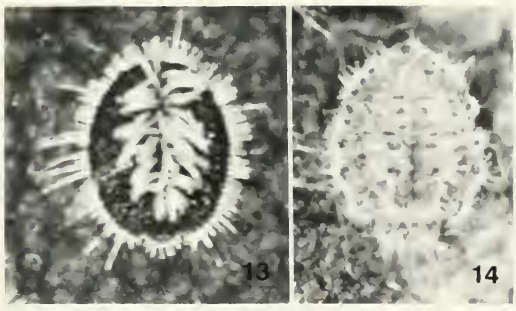
Description: **Fundatrix** (Figs. 11, 12): First Instar (Fig. 11). Body length 0.38–0.43 mm, width 0.19–0.25 mm. Dorsal wax pores large, in medial and marginal rows. On abdomen, dorsomedial wax pores usually 2 pairs each on segments 3 and 4 and 1 pair each on segments 6 and 7. Adult (Fig. 12). Color in life dark purplish brown, broadly oval to almost round. Eye a triommatidion. Apterous, body length 1.32–1.98 mm, width 0.94–1.42 mm. Dorsal cephalic setae length 0.8–1.6 × middle width antIII. Two pairs of thoracic spiracles; 4 pairs spiracles on abdomen. Two pairs wax glands on dorsum between 1st and 2nd, 2nd and 3rd coxae. Cornicles absent. Antenna 3-segmented; segments I and II about equal in length and each with 2 setae, segment III 0.114–0.193 mm long and 2.1–3.2 × length hindleg tarsal segment II (tIIh) with 2–3 short sensory pegs ventrally near apex, and 4 short thick apical with length 0.41–0.67 × middle width antIII. Rostrum length 0.8–1.5 × length antIII, reaching between 1st and 2nd coxae, rostral segment II with 6 setae, III with 2 setae; ars width : length 0.57–1.1 and length 0.65–1.3 × length cauda, bearing 8 setae, longest seta 0.33–0.7 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.18–0.25 mm long with 6 setae in a circle around the apex and 2–5 additional setae along its length; longest tibial seta 0.73–1.5 × middle width tibia. Hindleg femur length 0.9–1.1 × length tibia with 2 short setae on the anterior margin, 2 thick, blunt and 2 longer setae on apical margin and 0–2 additional setae. Hindleg tI setal pattern 2:2:2, longest seta tI hindleg 0.26–0.63 × length ventral margin tIh. Hindleg tarsal segment II 0.049–0.070 mm long and 0.23–0.31 × length tibia, with (all legs) 2 pair short setae and apically 2 long thick capitate setae (length 0.64–0.82 × length tIIh) and 2 thinner, shorter tapered setae. Length femur foreleg 0.72–0.87 × femur hindleg, setae as in hindleg except 1–2 in addition to 6 invariant; tibia foreleg 0.63–0.79 × tibia hindleg, setae as in hindleg except 0–4 in addition to 6 apical. Length femur midleg 0.76–0.92 × hindleg femur, setae as in hindleg; length tibia midleg 0.60–0.79 × hindleg tibia, setae as in hindleg except 0–2 in addition to 6 apical. Genital plate with 10–18 setae, longest seta 0.44–1.0 × longest caudal seta. Anal plate bilobed with 5–7 setae each lobe, longest seta 0.8–1.3 × longest caudal seta. Cauda rounded, 2.1–3.0 × broad as long with 3–8 (usually 6) setae, longest seta 0.5–0.9 × length cauda.

Alate Viviparous Female, Fundatrigenia or Emigrant (Figs. 20, 21): Color in life: Adult, thorax dark purplish brown to black; wings opaque, veins gray-brown. Eye, compound. Alate, body length 1.25–1.93 mm. Dorsal cephalic setae 5–13, longest 0.58–1.085 × constricted basal width antIII. Ventral cephalic setae 5–11. Two pairs of thoracic spiracles; 4 pairs abdominal spiracles. Cornicles absent. Length forewing 1.9–2.2 mm, medius unbranched, width cu-1a 0.9–1.4 × width medius, width cu-1b 1.0–1.7 × medius. Hindwing 1.0–1.4 mm long with medius only, hooklets 2–3. Antenna 3-segmented; length segment I 0.8–1.5 × segment II and each segment with 2 setae, segment III 0.36–0.52 mm long and 4.4–6.3 × length tIIh and bearing 26–40 annular sensoria (Figs. 20, 21), 2–3 short thumb-

Figs. 11, 12. *Hormaphis cornu* fundatrix. 11, 1st instar. 12, Adult.

like projections ventrally near apex, and 4 short thick apical projections, longest 0.86–1.18 × constricted basal width antIII. Rostrum (segments II–V), length 0.35–0.46 × length antIII, reaching just past 1st coxa, setae as in fundatrix; ars width : length 0.7–1.3 and length 1.05–1.49 × length cauda, longest seta 0.24–0.51 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.35–0.44 in length with 6 setae in a circle around the apex and 21–35 additional along entire length, longest tibial seta 0.68–1.07 × middle width tibia. Hindleg femur length 0.71–0.86 × length tibia, with 2 short setae on the anterior margin, 2 thick, blunt and 2 longer tapered setae on apical margin, and 3–15 additional setae. Hindleg tarsal segment II 0.075–0.090 mm long and 0.18–0.26 × length hindleg tibia, with (all legs) 2 pair short setae and apically 2 long thick capitate setae (length 0.41–0.70 × length tIIh) and 2 thinner, slightly shorter capitate setae. Length femur foreleg 0.81–0.93 × femur hindleg, setae as in hindleg except 5–17 in addition to the 6 invariant; tibia foreleg 0.69–0.79 × tibia hindleg, setae as in hindleg except 13–25 in addition to 6 apical. Length femur midleg 0.78–0.90 × hindleg femur, setae as in hindleg except 6–18 in addition to 6; length tibia midleg 0.70–0.79 × hindleg tibia, setae as in hindleg except 15–28 in addition to 6 apical. Tarsal segment I setal pattern 3:3:2, longest seta tI hindleg 1.3–2.2 × length ventral margin tI. Genital plate with 16–23 setae, 6–15 secondary and 10–18 marginal setae (no obvious primary setae), longest seta 0.48–0.98 × longest caudal seta. Anal plate bilobed with 5–7 setae each lobe, longest seta 0.63–1.15 × longest caudal seta. Cauda knobbed, 0.98–1.7 × broad as long with 7–10 (usually 10) setae, longest seta 0.67–1.1 × length cauda.

Apterous Aleurodiform Female (Fig. 13): Color in life: Shiny dark purplish black with white fringe of wax tubercles encircling body margin and scattered on dorsal midline. Head, thoracic, and abdominal segments

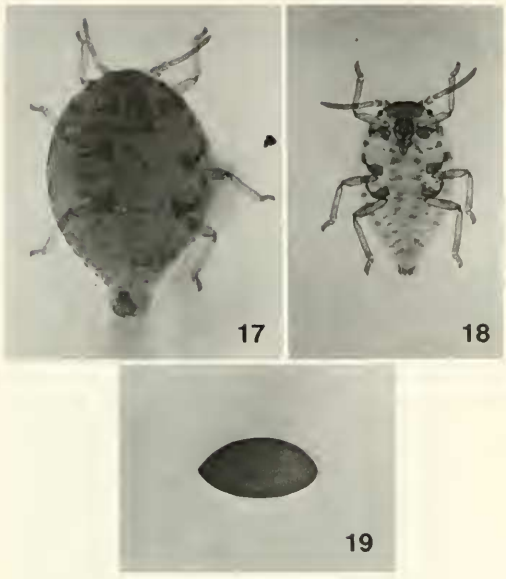


Figs. 13, 14. *Hormaphis cornu.* 13, Apterous alcyrodiform female. 14, 4th instar of sexupara.

Figs. 15, 16. *Hormaphis cornu* sexupara. 15, Wing venation. 16, Whole body.

fused to form broadly oval to almost circular body. Apterous (Fig. 13), body length 0.64–0.94 mm, width 0.55–0.77 mm. Eye a triommatidion. Ventral surface tightly adhered to leaf underside, exoskeleton with a brittle waxy coating. Tarsi on fore and middle legs absent, rudimentary on hind, claws absent. Antenna reduced, 2–3 segments. Rostrum reaches to 3rd coxae. Anal plate bilobed. Cauda rounded.

Sexupara or Immigrant (Figs. 14–16, 22–23): Color in life: Adult, thorax dark purplish brown to black; wings opaque, veins grey-brown. Eye, compound. Alate (Fig. 16), body length 0.88–1.44 mm. Dorsal cephalic setae 4–12, longest 0.59–1.53 × constricted basal width antIII. Ventral cephalic setae 4–9. Two pairs of thoracic spiracles; 4 pairs abdominal spiracles. Cornicles absent. Forewing (Fig. 15) length 1.29–1.93 mm, medius unbranched, width cu-1a 0.87–1.33 × width medius, width cu-1b 0.91–1.75 × medius. Hindwing (Fig. 15) 0.72–1.17 mm long with medius only, hooklets 2–3. Antenna 3-segmented; length segment I 0.87–1.28 × segment II and each segment with 2 setae, segment III 0.27–0.41 mm long and 4.2–5.9 × length tIIh, bearing 17–29 annular secondary sensoria (Figs. 22, 23), 2–3 short sensory pegs ventrally near apex, and 4 short thick apical setae, longest 0.87–1.59 × constricted basal width antIII. Rostrum (segments II–V), length 0.36–0.50 × length antIII, reaching to ⅓–½ distance to 2nd coxae, setae as in fundatrix; ars width : length 0.59–1.33 and length 0.97–1.44 × length cauda, longest seta 0.18–0.58 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.23–0.33 in length with 6 setae in a circle around the apex and 8–21 additional along entire length, longest tibial seta 0.65–1.15 × middle width tibia. Hindleg femur length 0.73–0.87 × length tibia, with 2 short setae on the anterior margin, 2 thick, blunt and 2 longer tapered setae on apical margin, and 0–5 additional setae. Hindleg tarsal segment II 0.055–0.077 mm long and 0.20–0.27 × length hindleg tibia, with (all legs) 2 pair short setae and apically 2 long thick capitate setae (length 0.56–0.80 × length tIIh) and 2 thinner, slightly shorter capitate setae. Length femur foreleg 0.70–1.18 × femur hindleg, setae as in hindleg except 5–17 in addition to the 6 invariant; tibia foreleg 0.58–1.05 × tibia hindleg, setae as in



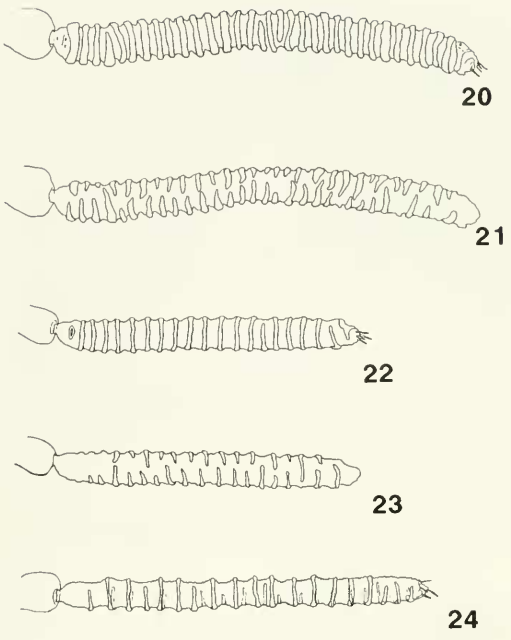
Figs. 17–19. *Hormaphis cornu* 17, Ovipara. 18, Male. 19, Overwintering egg.

hindleg except 2–12 in addition to 6 apical. Length femur midleg 0.66–1.15 × hindleg femur, setae as in hindleg except 1–9 in addition to 6; length tibia midleg 0.58–1.08 × hindleg tibia, setae as in hindleg except 3–14 in addition to 6 apical. Tarsal segment I setal pattern 3:3:2, longest seta tI hindleg 1.36–2.09 × length ventral margin tI. Genital plate with 8–21 setae, 4–8 secondary and 4–13 marginal setae (no obvious primary setae), longest seta 0.51–0.99 × longest caudal seta. Anal plate bilobed with 6–8 setae each lobe, longest seta 0.67–1.39 × longest caudal seta. Cauda knobbed, 1.13–1.61 × broad as long with 8–10 (usually 10) setae, longest seta 0.74–1.05 × length cauda.

Ovipara (Figs. 17, 27): Color in life: Juvenile covered with fuzzy grayish wax secretions, adults shiny purplish black. Apterous (Fig. 17), body pyriform, convex dorsally and flat ventrally, no tubercles or waxy secretions, highly sclerotized. Eye a triommatidion. Body length 0.86–1.15 mm, width 0.51–0.73 mm. Dorsal cephalic setae length 0.7–1.5 × middle width antIII. Dorsal body setae thick, slightly capitate, ventral tapered. Two pairs wax glands, between 1st and 2nd, 2nd and 3rd coxae. Two pairs of thoracic spiracles; 4 pairs abdominal spiracles. Cornicles absent. Antenna 3-segmented; segments I and II about equal in length and each with 2 setae, length segment III 0.18–0.29 mm and 3.0–4.4 × length tIIh, with 2–3 short sensory pegs ventrally near apex and 4 short thick setae on apex with length are 0.61–0.82 × middle width antIII. Rostrum length 0.54–0.85 × length antIII, reaching to 2nd coxae, setae as in fundatrix; ars width : length 0.75–1.1 and 0.7–1.3 × length cauda, longest seta 0.29–0.65 × width ars. Coxae of all legs with 6 setae. Tibia of hindleg 0.193–0.249 mm long with 13–31 round to oval pseudosensoria (Fig. 27); setae as in fundatrix except 3–9 in addition to apical 6, longest tibial seta 0.51–1.11 × middle width tibia. Hindleg femur length 0.79–1.03 × length tibia, setae as in fundatrix except 0–2 in addition to 6 invariant. Hindleg tarsal segment I setal pattern 3:3:2, longest seta tIh 1.5–2.3 × length ventral margin tIh. Hindleg tarsal segment II 0.052–0.071 mm long and 0.24–0.34 × length tibia, with (all legs) 2 pair short setae and apically 1 pair long thick capitate setae (length 0.52–0.79 × length tIIh) and 1 pair thinner, slightly shorter capitate setae. Length femur foreleg 0.89–1.04 × femur hindleg, setae as in hindleg except 1–6 in addition to 6 invariant; length tibia foreleg 0.75–1.0 × tibia hindleg, setae as in hindleg except 3–12 in addition to 6 apical. Length femur midleg 0.89–1.04 × hindleg femur, setae as in hindleg except 1–3 additional; length tibia midleg 0.77–1.03 × hindleg tibia, setae as in hindleg except 4–13 additional. Genital plate with 13–31 setae, longest seta 0.63–1.12 × longest caudal seta. Anal plate bilobed with 6–8 setae each lobe, longest seta 0.84–1.4 × longest caudal seta. Cauda knobbed, 1.0–1.6 × broad as long with 10 (rarely only 5 or 6) setae, usually 2 longer than the rest, longest seta 0.97–1.7 × length cauda.

Male (Figs. 18, 25): Color in life: Juvenile

and adult as in ovipara. Apterous (Fig. 18), body dorsoventrally flattened, elongated pyriform in shape, no tubercles or waxy secretions, highly sclerotized. Eye a triommatidion. Body length 0.56–0.74 mm, width 0.32–0.41 mm. Dorsal cephalic setae length 0.44–1.11 × middle width antIII. Dorsal body setae as in ovipara. Two pairs of thoracic spiracles; 4 pairs abdominal spiracles. Two pairs wax glands as in ovipara. Cornicles absent. Antenna 3-segmented; segments I and II about equal in length and each with 2 setae, segment III 0.19–0.24 mm long and 3.3–4.6 × length tIIh, with 13–22 short sensory pegs (Fig. 25) ventrally and 4 short thick setae on apex which in length are 0.42–0.71 × middle width antIII. Rostrum length 0.50–0.71 × length antIII, reaching between 2nd and 3rd coxae, setae as in fundatrix; ars width : length 0.79–1.28 and 1.0–1.5 × length cauda, longest seta 0.30–0.63 × width ars. Coxae all legs with 6 setae. Tibia of hindleg 0.176–0.211 mm long, setae as in ovipara except 3–11 in addition to apical 6, longest tibial seta 0.61–1.56 × middle width tibia. Hindleg femur length 0.74–0.92 × length tibia, setae as in fundatrix except 0–2 in addition to the 6 invariant. Hindleg tarsal segment I setal pattern 3:3:2, longest seta tIh 1.5–2.6 × length ventral margin tIh. Hindleg tarsal segment II 0.047–0.062 mm long and 0.26–0.33 × length tibia with setae as in ovipara; length thick capitate setae 0.64–0.82 × length tIIh. Length femur foreleg 0.91–1.04 × femur hindleg, setae as in hindleg except 1–3 in addition to 6 invariant; length tibia foreleg 0.76–0.88 × tibia hindleg, setae as in hindleg except 1–5 in addition to 6 apical. Length femur midleg 0.92–1.01 × hindleg femur, setae as in hindleg except 0–3 additional; length tibia midleg 0.80–0.91 × hindleg tibia, setae as in hindleg except 1–6 in addition to 6 apical. Anal plate bilobed with 5–8 setae each lobe, longest seta 0.7–1.1 × longest caudal seta. Cauda knobbed, 0.91–1.37 × broad as long with 6–9 setae, longest seta 0.66–1.2 × length cauda.

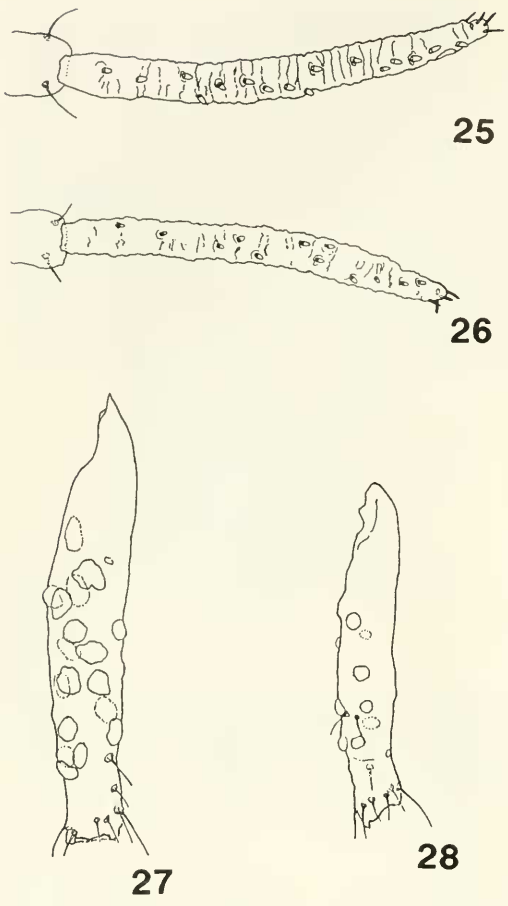


Figs. 20–21. *Hormaphis cornu* alate viviparous female, antennal segment III. 20, Ventral view. 21, Dorsal view. Figs. 22–23. *Hormaphis cornu* sexupara, antennal segment III. 22, Ventral view. 23, Dorsal view. Fig. 24. *Hormaphis hamamelidis* sexupara, antennal segment III.

Overwintering egg (Fig. 19): Pale orange yellow when first laid, then darkening to shiny black, 0.43 mm long and 0.22 mm diameter.

Gall: Conical but usually constricted at the base, tapered tip often bent to one side, protruding from upper leaf surface and usually on a major leaf vein; length from tip to base on leaf underside 8.2–19.4 mm (mean = 13.5) and 4.0–8.1 mm (mean = 5.6) at greatest width. Underside of gall on lower leaf surface circular and somewhat swollen beyond leaf; the opening at first obstructed by plant hairs, later forms a small circular exit hole. Color pale green, turning yellow in early summer.

Biology: Fundatrices hatch in late March from overwintering eggs laid on the bark of witch-hazel, form cone-shaped galls on leaves and produce virginoparous emi-



Figs. 25–28. 25, *Hormaphis cornu* male, antennal segment III with sensory pegs. 26, *Hormaphis hamamelidis* male, antennal segment III with sensory pegs. 27, *Hormaphis cornu* ovipara, hind tibia with pseudosensoria. 28, *Hormaphis hamamelidis* ovipara, hind tibia with pseudosensoria.

grants into mid-June. Alate virginoparae depart from galls in June and migrate to river birch to produce the first aleurodiform generation on the undersides of leaves. Two more aleurodiform generations follow; the last produces sexuparous nymphs. Mature sexuparae depart from leaves of river birch and fly back to witch-hazel in mid-September to early October and deposit sexual nymphs. Sexuales mature in late September to late October and mate. Ovipara produces several overwintering eggs which are laid in crevices in the bark or occasionally at the base of leaf buds. See von Dohlen and Gill (1989) for additional information.

Types: Location unknown.

Material examined: On witch-hazel, Dranesville District Park, VA, C. D. von Dohlen: 4 fundatrices in May 1985, 1 fundatrix and 3 alate virginoparae on 30 May 1985; alate virginoparae, 6 on 5 June 1985, 20 on 6 June 1986; 1 oviparae in October 1985, 8 oviparae and 16 males on 17 October 1985, 3 oviparae on 24 October 1985, 10 oviparae and 12 males on 1 October 1986. On witch-hazel, U. S. National Arboretum, M. B. Stoetzel: 9 oviparae and 2 males on 22 October 1987. On river birch, Dranesville District Park, VA, C. D. von Dohlen and M. B. Stoetzel: 2 alate virginoparae on 4 June 1985; 24 apterous virginoparae on 18 August 1985.

Summary

Hormaphis hamamelidis forms small, conical galls usually without basal constriction, is autoecious on witch-hazel, and lives at high elevations in northern regions of the eastern United States. *Hormaphis cornu* forms larger, conical galls that are usually constricted at the base, is host-alternating between witch-hazel and river birch, and is found at low elevations in the mid-Atlantic and southern regions of the eastern United States.

Correction of Names in Previous Papers

The correct species designations may be sorted out as follows. Because of their northern location (New York State) and the dates of the occurrence of alates in conical galls on witch-hazel, the aphids described by Fitch (1851) must be the autoecious species. The original generic designation by Fitch was incorrect. The species belongs in *Hormaphis* Osten-Sacken, and the correct name for this aphid is *Hormaphis hamamelidis* (Fitch 1851). The aphid Osten-Sacken (1861) described from the Washington, D.C. area was

the host-alternating form. However, because the specific name *hamamelidis* is preoccupied, Osten-Sacken's designation is a secondary homonym of *hamamelidis* Fitch 1851 and is not available. The data on antennal sensoria given above indicate that Shimer's (1867) description of *Hamamelistes cornu* unquestionably is the same host-alternating species studied by Osten-Sacken (1861). Therefore, *cornu* Shimer is the first valid, available name for the heteroecious species. The species belongs in *Hormaphis* Osten-Sacken, and the correct name for this aphid is *Hormaphis cornu* (Shimer 1867). *Hormaphis cornu* (Shimer) is the correct name for the heteroecious species treated by Pergande (1901) and von Dohlen and Gill (1989).

Disposition of Species in *Hormaphis*

Consistency in generic distinctions should be extended to other species of the tribe Hormaphidini. As treated here, *Hormaphis* is distinctive in its unusual antennal segmentation (3 segments) and the venation of the hindwing (no cubitus), and is solely a North American genus with two species. We have seen specimens of *betulinus* Horváth (1896), *gallifoliae* Monzen (1929), *kagamii* Monzen (1929), and *betulinus* subsp. *miyabei* Matsumura (1917), and examined descriptions of other species placed in Hormaphidini. Other than the two species treated here, all Hormaphidini are native to Japan or Europe, have 5-segmented antennae, and a cubitus vein in the hindwing. Thus, *Cerataphis betulae* Mordvilko (1901), *Mansakia gallifoliae* Monzen (1929), *Hamamelistes gibberi* Monzen (1954), and *H. gibberi* biological race *grossae* Monzen (1954), placed in *Hormaphis* by Eastop and Hille Ris Lambers (1976), all belong to *Hamamelistes.*

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